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Observations on the Development of the Excretory System in Turtles.

A Dissertation

submitted to the Faculties of the Graduate Schools of Arts, Literature, and Science, in Candidacy for the Degree of

Doctor of Philosophy
(Department of Zoology)

by

Emily Ray Gregory.

With 6 Plates and 1 Textfigure.

Jena,
Gustav Fischer.
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The researches described in the following thesis were carried on at the Hull Biological Laboratory of the University of Chicago, under the direction of Professor WILLIAM MORTON WHEELER whose suggestions have been most valuable. To him and to Dr. C. O. WHITMAN, Head-Professor of the Department of Zoology, I wish to express my deep appreciation of the kindness shown me and my sincere gratitude.

Material.

Early in the spring of 1897 Prof. WILLIAM MORTON WHEELER advised me to make a careful study of the development of the excretory system of the Turtle. For this purpose the late Prof. GEORGE BAUR gave me a number of embryos of *Aromochelys* and of *Platypeltis spinifer*, preserved in alcohol. On sectioning these, however, it proved that they were all too far advanced to show the origin of the excretory system, and it was necessary to seek more material, especially in the earliest embryonic stages. Through the courtesy of Prof. CARL H. EIGENMANN of Indiana University I gained access to its Biological Station at Vawter Park, Indiana, on the north side of Turkey Lake. My first visit was from noon of Friday, June 25th, 1887, until Monday the 28th. In this short time, with the help of two of the students, I collected between three and four hundred eggs. Of these I killed a few, some in chromic acid, and some in saturated solution of corrosive sublimate. Packing the rest carefully in a basket

with sand and decayed wood, I carried them back to Chicago in my hand. Unfortunately, I was just then forced to leave Chicago for three months, but the eggs were, through Dr. WHEELER's kindness, kept in the laboratory for me, and the embryos killed from time to time during July and August. On sorting this material carefully, after my return in October, I found few very young stages of *Aromochelys* and no advanced stages of *Platypeltis*, so that many of the *Platypeltis* eggs must have come to some sad fate. This material busied me during the winter of 1897—98, and in the summer of 1898 I went again to Vawter Park, staying from July 5th until August 11th. For several reasons, mainly because it was a little late and the nesting places had already been searched by others, I did not procure many young stages of either kind of turtle, but secured a fine lot of embryos of *Platypeltis* from 10 mm long up to the hatching time, making with those of the year before quite a complete series of this species. Returning to the University, my time since August 11th 1898 has been given to the preparation and study of this material. It would seem that the turtle cannot be very sensitive to adversity even in its embryonic condition. Of twenty-seven series cut before the end of November, none had to be discarded and but two or three show injured tissues, or abnormal conditions.

During the past summer almost all my material was fixed in chromic acid, 1%, or in sublimate acetic (KAISER's formula). There was no running water at hand, so I was forced to wash the chromic material as best I could by using large quantities of water and changing it frequently. The sublimate material was washed in 70% alcohol, with iodine added and hardened in 95 % or absolute alcohol. All the material was preserved in alcohol of 70 % or 85 %. A few embryos were killed in chrom. os. acetic, a few in nitric, and a number in picric acid. The sections, with few exceptions, were cut 10 μ thick. For my present purpose I have found iron haematoxylin followed by orange G the most satisfactory stain, although I have also used DELAFIELD's haematoxylin, borax carmine and picrocarmine.

The youngest stage (I) which I have preserved shows the beginning of the embryonic shield. Stage II consists of embryos of from 2.8 to 4.5 mm in length, which have from 9 to 15 somites. Stage III contains embryos 6.5—7 mm long with from 11 to many somites. The lens of the eye is invaginated and the head bending. Stage IV has embryos from 6.8 to 8 mm long, and somites are formed to the end of the body. In stage V the limb buds are conspicuous.

Stage VII is 8 mm long and the head is bent. Stage VIII is 9 mm long. The head and the tail are bent. Stage IX shows the first trace of pigment in the eye. Stage XVI has a carapace 7 mm long and a marked neck. The body is thick, the limbs slightly bent and the feet show the first signs of the formation of toes. The head is more than half as large as the body and the eyes are very large.

Individuals differ somewhat from the typical condition, especially in the younger stages. For here as in other forms, the size, particularly the length, does not accurately indicate the development of the organs, which varies considerably in individuals of apparently the same age. The stages are numbered with the Roman numerals beginning with the youngest. There are many gaps much greater than I could wish, chiefly in the younger stages. I have used the *Platypeltis* embryos almost exclusively in this study.

Researches.

In the study of the origin of the pronephros and of the pronephric duct, the embryo of the shark has been considered most valuable on account of the ancestral position of the shark in the Vertebrate phylum, and has been the object of much research. The turtle, also, as the one of the oldest of the Amniotes, is a very interesting form for the study of this subject. It should be good ground for solving the theoretical problem as to whether the entire excretory system, embryonic and adult, consists of three parts of one organ, or whether there are really three distinct organs, as well as the questions of origin which are involved in such a study.

In the present discussion I shall give first the results of my own observations, following the order of development, and beginning with the pronephros. A comparison of my results with those of other workers and the theoretical conclusions suggested by this study will follow.

Pronephros.

Stage II.

The basis of the pronephros in turtles is seen in my youngest embryos of stage II. It arises as solid outgrowths, at first like swellings, in the somatic region at the posterior end of the somites. These grow backward and overlie those following with which they soon fuse. The fourth somite (behind the ear) and the tenth seem to be the

anterior and posterior limits, respectively, of the organ. In only one case have I found clear indications of the pronephric basis between the third and fourth somites and a careful study of that embryo indicates that the segmentation towards the head has been retarded and that these somites, therefore, correspond to the fourth and fifth in other embryos. In none have I found the basis extending beyond the tenth somite. The individual embryos vary considerably as to the position of the anterior end of the basis, which on one side (it may be either one) almost invariably extends farther forward than on the other.

In *Aromochelys* II (3) the first slight swelling appears on one side at the end of the fourth somite. At the end of the fifth somite it is less distinct and only at the sixth is it pronounced on both sides. From this point it forms a conspicuous welt. The drawings of this embryo on Plate 1, Figs. 1—14, will make the condition quite plain. The first section of somite VI (Fig. 1) shows the very edge of the somite. There is no sign of any swelling on the somite and the side plates are quite flat. Section 5 of the same somite (Fig. 2) shows a wider connection between somite and middle plate. The upper part of this is due to the proliferation, from the somite, of cells for the pronephric basis. Two sections further back we see that the welt is a conspicuous feature, and by internal growth pushes up and against the ectoderm. Section 8 (Fig. 3) is near the end of the somite, but the ridge remains and even increases. Sections 9 and 10 (Figs. 4 and 5) show how this welt bridges over the space between the two somites, and beneath, as in two sections before, the cells which form the walls of the aorta can be seen slipping out from the splanchnic mesoderm and lying beneath the somite. In section 6 of somite VII (Fig. 6) we see the pronephric welt reenforced, for in this case the basis is still fused with the somite throughout. In section 10 (Fig. 8) we see the same bridge as before, although the right side is a little lower. The sixth section of somite VIII (Fig. 9) shows again most clearly how the basis of the pronephros is a direct outgrowth from the somite. The arrangement of the cells makes it still a part of the somite. Here, too, on the left, we see that this solid extension from the somite is gaining a lumen which will open into the coelom beyond. From this point the ridge gradually lowers, though we still clearly see it as a rudiment in the tenth somite. Beyond this the embryo is unsegmented, and on the right the last sign of the pronephric welt is seen. Section 10 of somite VI (Fig. 18) really lying

between the sixth and seventh somites, shows the relative position of pronephric and mesonephric bases. We see here the middle piece on the left, thickened and showing a mitotic figure. There is no sign yet of the pronephric duct, excepting as the basis of the part usually called the collecting duct, is involved in the ridge described. The same stage is seen in *Aromochelys*, II (1).

A slightly later stage, showing the beginning of the pronephric duct is seen in B, II (1) (Plate 2, Figs. 1—10). Here a complete ridge is not formed and we can follow the separate outgrowths more easily. In somite V, section 9 (Fig. 1), we see the first outgrowth, extending with a peculiar enlargement on the left in somite VI, section 1 (Fig. 2), to lie above the outermost cells of the second outgrowth in VI, 8 and 10 (Figs. 3 and 4). The second reaches over somite VII to the fifth section and probably the tip fuses with the third outgrowth seen in VII, 6—11 (Figs. 6—8). In somite VIII (Fig. 9) the fourth outgrowth is seen and from this the duct extends, the outgrowth dwindling in the ninth somite (Fig. 10). The enormous number of mitotic figures in this embryo is very striking. They have all been drawn in with the camera; the other cells were added free hand.

In this case, the fusion of the duct with the ectoderm is of considerable extent and very marked. In most of the cases I have so far observed it is not so easily detected. It is undoubtedly let into the ectoderm, having near the end a sheath of ectoderm over it on the inner side, while that seen anteriorly between ectoderm and duct has disappeared. Whether there is a genetic relation here between the ectoderm and the tip of the duct is not perfectly clear from the preparations studied hitherto. MITSUKURI says he has proved this fusion "beyond the possibility of a doubt". On Plate 1, Figs. 27 to 29 will be found drawings of the ends of the duct in two embryos.

In B, II (1) (Plate 2, Figs. 1—10) the origin of the first walls of the dorsal aorta from cells escaping from the sclerotome is again very distinct.

As we proceed to the later stages, however, a new factor comes in which greatly modifies these conditions. Before there is more than a hint of a lumen in the pronephric tubules, we see in some of the same somites (from the second pronephric tubule on), as well as further back, at the point where they pass into the middle plate, marked thickenings. These are the bases of the mesonephric tubules. See B, II, 1, somite VII (Plate 1, Figs. 15—17). They become more

and more distinct, until in some series we find the pronephric tubule and that of this mesonephric rudiment (now as distinct as the other), opening side by side into the body cavity, but further back and in older embryos, we find the pronephric funnels opening into these rudiments of the mesonephric funnels and through them into the coelom. These conditions may be seen in *Platypeltis*, II (5) and II (7). In embryo II (5) in somite V, section 9, we see the rudiments of the pronephric tubules (on the right apparently two) and of the mesonephric tubules from the middle plate opening into the coelom, while the splanchnic sheets then again bend in and push as far as they can under the aorta. In somite VI, sections 12 and 13, we see that these rudiments of the pronephros and mesonephros no longer have separate openings, but fuse and have but one opening. The great irregularities which occur may also be seen by a study of this series. The duct is present as a solid rod. In embryo II (7) (Plate 1, Figs. 19—26) similar conditions will be found, markedly in somite VII, sections 6 and 7 (Figs. 19 and 20), and in somite VIII, sections 5 and 7 (Figs. 21 and 22). Here too, the beginning of the duct is seen.

Thus it becomes clear that although the pronephros is distinct in origin, and arises as segmental outgrowths from the somites and extends over but few segments; the mesonephros, arising from the middle plate, extends almost as far forward as the pronephros and after the earliest stages have passed, the two are so fused that the parts cannot be distinguished. It is also clear that we have here the same relative positions as in the shark. It will be noticed also that, although of segmental origin, even at this early stage irregularities appear, and we frequently find more than one tubule in a somite. Thus in II (7) the seventh somite has two tubules on each side, and the eighth has two on the right side.

Stages III—VI.

At this time the anterior tubules, especially those which end blindly, are quite simple and straight, but the posterior ones become longer and somewhat twisted and S-shaped. The walls of the tubules are formed of thickly-packed, cylindrical cells, which stain very densely. There is no appreciable distinction between the cells of the duct where it appears and those of the tubule. Mitotic figures are also sometimes seen in the tubules, but not so frequently as we should expect from the great increase in size and length, which takes place after this time. The enormous growth in the size of the single cells

would alone account for a considerable amount of the growth in length but I doubt whether it will account for all of it.

To show the number of funnels not finally closed off from the coelom in these stages we may tabulate the conditions found in several embryos:

III (4)	Som. 5	6	7	8	9	10		
Funnels	R	2	3	3	2		Total	10
„	L		4	2	2		„	8
IV (1)	Som. 5	6	7	8	9	10		
	R	1	2	2	3	2	Total	10 or 11
	L	1	2	3	3	2	„	11 or 12
V (2)	Som. 5	6	7	8	9	10		
	R	1	3	4	3	2	Total	13
	L		1	3	2	1	„	7
VI (2)	Som. 5	6	7	8	9	10		
	R	1	3	3	5	2	Total	14
	L	1	3	2	4	2	„	12

From what has been said above it is obvious that beyond the sixth somite which seems to be the anterior limit of the mesonephros, one cannot say how many of these tubules are pronephric. On account of their segmental origin we should expect that there would be only six pronephric tubules, but as the fusion with the mesonephric elements comes in before the tubules are fully formed, it is impossible to say whether the increase in number is due to this factor alone or not.

In stages III—VI, Plates 2 and 3, there are in some cases several funnels (1—3) before there is any sign of a continuous duct. On the other hand, in some cases we find the duct continuous from the first tubule which appears. This may be on either side, as indicated by the irregular appearance of the basis, or, more rarely, the first tubules may be nearly opposite. The so-called "collecting duct" is therefore very imperfect, here, as a rule. In the pronephric region, the duct is evidently formed by the fusion of the tip of each tubule with the tubule following. Further back, the duct seems to develop by the division of its own cells or through genetic relation with the ectoderm as indicated above. As early as stage III the duct reaches and opens into the cloaca.

In the majority of embryos older than II, as noted before the pronephric tubules and the mesonephric tubules in the same region open into the coelom by a single funnel. This opening generally becomes more and more median and more contracted until at the end

of the pronephric region it has closed and the tubule is entirely cut off from the coelom. This fact will be considered again under the discussion of the mesonephros. There are, however, interesting exceptions to this fusion of pronephric and mesonephric elements and to the median position of the posterior funnels. First, in some embryos we find tubules with two distinct funnels, sometimes widely separated, evidently the pro- and mesonephric funnels, with but one opening into the duct and in one case, at least, the tubules remain separate although extending over almost the same sections, see embryo III (5), somite VII, sections 3—10 (Plate 2, Figs. 11—18). Again, where the funnel is single we find sometimes, notably in embryo VI (2), the tubule extending on one side to the duct and on the other towards the aorta, where we see clearly the widening of the end of the tubule to receive the glomerulus, at this time unformed or represented by irregular tufts of very typical cells.

Here, too, we find branches from the aorta running to the tubules and the formation of a glomus. The aortic branches start from the lower part of the aorta on each side. In two apparently normal embryos, III (4) and III (5), several of them are opposite each other, but in no case do the branches of the two sides correspond exactly, either in size or number. In III (4) there are nine on the right and five on the left. In Embryo III, 5, somite VI, 7, there may be seen two pocket-like evaginations from the aorta, opposite each other. Anterior to this there is but one tubule on the left side, but beyond this point they are on both sides. The aortic branches can be seen again in VII, 5, 6, 7 (Plate 2, Figs. 13—15), and in VIII, 13. In all there are seven branches on the right and nine on the left. The lacunae here are rather small, and may be seen in sections VI, 6, VIII, 3, and others. In both cases III (5) and III (4) the first aortic branch is in the sixth somite. In one, they end in the ninth, and in the other, in the tenth somite. In Embryo V, 2 the lacunae are much more conspicuous, noticeably in somites VIII and IX, see Plate 3, Figs. 2 and 3; and other series show them even more strikingly. Another embryo IV (1), also apparently normal but more advanced than the former, has fifteen aortic branches on the left, and only eight on the right, beginning in the fifth and ending in the tenth somite. Still another, IV (5), is very much behind in this respect. It has only one aortic branch on the right and five on the left, with the first point-like beginnings of others. These aortic branches, which begin as pointed or pocket-like evaginations from the aorta,

vary in width from ten to ninety mikra, more frequently from twenty to forty mikra. They extend down towards the inner ends of the tubules and push out the endothelium of the coelom, forming bubble-like lacunae around the tubule and chiefly about the opening of the funnel into the coelom. Towards the end of the pronephric region it is, at first, often difficult to tell whether the tubule has been cut off from the coelom or whether the opening is merely covered by the lacunae which are distended (perhaps temporarily) from either side until they meet (see Plate 3, Figs. 1—3). A careful study shows that even if the lacunae of the glomus meet across the funnel, liquid from the coelom could readily pass through their loosely built walls. Furthermore, at the tenth somite, the lining of the coelom, passing solidly across this region, with close-set cubical cells, not only closes the funnels but confines the lacunae of the glomus over the short distance they still continue. Therefore, this last condition alone can be considered as the actual closing off of the tubules (see Plate 3, Fig. 4). Exceptionally in the ninth somite of embryo IV (1) there is one closed funnel before the first open one and a second closed funnel between the first and second open ones.

In embryos of stage IV and older ones we see in the last somite of the pronephric region the first appearance of the glomeruli. They lie within the tubules and overlap for a short distance the glomus already described. This first appearance of the glomerulus is seen in Embryo V (2), somite X, section 9 (Plate 3, Fig. 4). The description will be found under the head of the mesonephros.

Stages VII—XVI.

The specimens now prepared of stages VII and VIII are clearly abnormal, and stages IX and X of *Platypeltis* are wanting. We will therefore next consider stages XI and XII. Here we find the following differences in the pronephric region. The coelom does not extend so far forward and we find the nephric elements at the extreme point of the coelom, and even extending into the sclerotome anterior to it. Embryo XII, 4, shows as the most anterior nephric element, the duct beginning on the left at the fourth section of the seventh somite, imbedded in the sclerotome. In the eleventh section we come to the end of the coelom, and here there is a rudiment of a tubule also. At the twenty third section, a distinct nephric basis is seen on the right side. The lacunae are more or less filled up with vascular tissue, giving the glomus the appearance of vascular tufts, extending into the coelom, or closed off by the endothelium at the tenth somite.

Some cilia can be found in stage VII and from stage XI they are always found. What cursory examination I have made of them indicates that each cell in and about the mouth of the funnel and for varying distances up the tubule (at times almost to the duct) has one large strong cilia. They can still be seen in embryo XVI (1) (Plate 6).

Even the most anterior tubules at this stage show the cells greatly increased in size, with clearer, lighter, more glandular appearance, and many of them containing dark staining granules. Many blood corpuscles are now found in the glomus. The increased size of the tubules and of the cells of necessity pushes out the endothelium, so that, except at the very anterior end, we have a decided kidney lobe. The development of the tubules and of the glomera may be seen in the drawings of *Platypeltis* embryo XII (3) [Plate 3, Figs. 5—9]. I have drawn somewhat more of the body than was necessary in order to show the relative position of the parts at this stage. It is somewhat difficult to follow the somites exactly by the time we have reached this stage, and thus the later history of the pronephric region is difficult to determine positively. It appears to me, however, that the whole is pushed back and crowded into a small space, as the head and neck develop, but that, nevertheless, the front end is overtaken by the sclerotome, and cut off from the coelom. This gradually degenerates though the arrangement of the cells may remain for a considerable time.

In a somewhat older embryo we find that all the tubules still showing an opening into the body cavity (although very small) lie within three somites. In stage XVI, what remains of the pronephric region may readily been seen in the sagittal drawing, Plate 6, which shows the pronephric glomi still hanging free in the body cavity at the anterior end of the mesonephric lobe. Other sections of the same series show four tubules opening into the coelom at this place.

Briefly, the pronephros is composed of tubules, arising segmentally from the somatic layer of somites 4—10, but early becoming more numerous, which on the median side open into the coelom and outwards either end blindly or open into the duct formed by the fusion of their ends. The funnels and lower parts of the tubules are surrounded by lacunae furnished with blood from the aorta, which may anastomose from point to point, and which in later stages acquire some tissue and push out into the body cavity as external glomera.

Mesonephros.

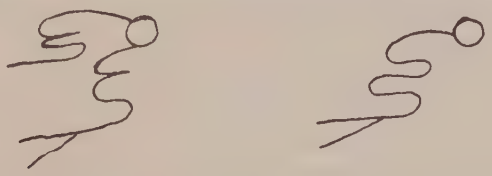
Owing to the fusion of the anterior part of the mesonephros with the pronephros, this region of the former has already been described. For the sake of clearness, however, we may repeat somewhat. The basis of the mesonephros in the turtle lies in the middle plate and may reach as far forward as the sixth somite, but the position of the anterior end seems to be variable. The first indications of its appearance may be seen in the camera drawings of the embryo B II (1) (Plate 2, Figs. 1— 10) already referred to. In the pronephric region, the tubules of the mesonephros fused with those of the pronephros or lying alongside, as before stated, open into the coelom. These openings, or "funnels", as they are commonly termed, from a lateral position become ventral, and often finally as close to the median line as possible, the aperture at the same time decreasing in size. From the tenth somite on, the tubules are entirely cut off from the coelom, ending blindly near the aorta.

It is, perhaps, impossible to be certain of the reason for this, but it will be well to consider the conditions, which may be, at least in a measure, causal. The pronephric welt arises at a time when the embryo lies quite flat upon the yolk. The ectoderm extends only just over the middle plate, and is drawn up and back again above the embryo to form the amnion. The somatic layer of the mesoderm follows it closely, while the splanchnic layer is equally close to the entoderm. The result is that the two layers of the mesoderm thus stretched apart are quite widely separated even to the middle plate, where a notch marks the end of the splitting of the single mesodermal sheet. Besides there is as yet no distinctive endothelial layer, so there is little hindrance and every help to the opening of nephric tubules into the coelom. As the embryo grows, the development of the aorta and its increasing size raise it up above the yolk, and the outer corner of the somites comes to point almost ventrally, bringing the mesoderm with it. The folding together of the sides of the intestine draws the mesoderm still further in the median direction. This growth and development early overtakes and runs ahead of the nephric growth and at least favors, if it does not cause, the fusion of somatic and splanchnic layers at the point where they leave the middle plate. Then follows the gradual differentiation of the layer next the body cavity to form a single sheet, lining it and separating the mesonephric tubule basis from it.

The pronephric region ends with the tenth somite where we sometimes find the two overlapping elements clearly differentiated, therefore, we have in somite XI the beginning of the purely mesonephric part. This extends through the body to the opening of the Wolffian duct into the cloaca. In stage II (with perhaps one exception where the end is injured) the division into somites has not yet been completed and the duct does not reach the cloaca. Here the mesonephric basis may be distinguished as far as the somatic division extends and perhaps a little beyond, by the thickening of the middle plate and the large number of mitotic figures in it. In stage III the duct has reached the cloaca and the mesonephric blastema is clearly laid down to the end. There are no tubules with a lumen opening into the duct beyond the tenth somite, and from this point on, the blastema extends as a rod of concentric, densely packed cells, its round shape modified from point to point where the tubules are growing towards the duct. In these places there is often a small lumen, especially near the anterior end. In each of somites eleven and twelve of III (5) there seem to be two tubules developing and only the blastema beyond. In the posterior part of III (4) I also noted two tubules to a somite. In IV (1), however, which is more advanced, I counted ten on one side and on the other thirteen more or less rudimentary tubules beyond the pronephric region, but the arrangement was very irregular. The tubules continue to develop successively backwards and the continuity of the blastema as well as its original shape disappears. But the growth of the skeleton and other organs cramps the posterior end so that the tubules cannot develop and here for a short distance there remain only the solid rudiments of tubules and perhaps finally only a very small irregular, rod-like blastema.

Passing over, at least for the present, stages VII, VIII, IX and X, we come to XI and XII. Here we seem to have a regularly developed stage of the mesonephros but one not yet very complicated in its structure. The number of the tubules in a somite is variable. Taking *Platypeltis*, XII (3), of which the pronephric region is found on Plate 3, Figs. 5—9 for our type, we find the following conditions: In the eleventh somite there are five tubules on the right, and four on the left; in the twelfth, thirteenth and fourteenth, three on each side. In these somites, we find the form of tubule which has been typical up to this stage. On the right it is an S spreading into a funnel at its lower end to receive the glomerulus, and opening into

the duct at its tip. On the left, of course, it is the S reversed. Sometimes a second bend is found in the upper half. In the fifteenth somite there are four tubules on each side; the second on the right and the third on the left show a further differentiation. Here the tubules on each side are doubled, the lower is the same as those seen before, generally with the second bend, and just above is a smaller one. This doubling continues as a tubule or rudiment through the rest of the organ. In the sixteenth somite there are four double



tubules on each side and in the third on the left side a small glomerulus is seen in the upper tubule, but this is the only one seen in the smaller tubules at this stage. Somite XVII has five double tubules; the glomerulus of the primary tubule is dwindling, and the cells of the tubules are smaller. Somite XVIII has four, and somite XIX six double tubules. In these somites the glomerulus has not yet appeared. In the twentieth somite the four double tubules are rudimental. In somite XXI the five double rudiments can no longer be called tubules. In somite XXII the rudiment is sometimes single but more distinct and double apparently where tubules would form if they had a chance. Sections three and four of somite XXV show the last remnants of the mesonephric basis. The opening of the duct into the cloaca extends over sections three to eleven of this somite. At section six the ureter opens into the duct. Beyond this point I counted twelve somites, ten in the tail, making thirty-five in all. The kidney lobe has become quite large and its endothelial wall consists of long flattened cells.

In an embryo of stage XVI (Plate 5, Fig. 1) further development is seen. Here there are very constantly three tubules on a side, one over the other, and three glomeruli. Sometimes there appear to be more. The duct here lies against the wall of the mesonephros with the cardinal vein just above, and the tubules can be found opening into the duct at any point not so covered. Beyond this stage the tubules become so numerous, crowded and twisted, that it would be most difficult to count them. The sagittal section seen in the camera drawing on Plate 6 also shows its structure in this stage.

A study of *Platypeltis* embryo XII (3), and of the following stages, indicates very clearly that the secondary and later series of tubules arise *in situ* from part of the original blastema. The beginnings of the secondary tubules can be easily followed and their independent character demonstrated. In this embryo there still remains considerable blastemic tissue around the tubules in the kidney lobe. In stage XVI, however, on the outer and lower sides of the lobe we find only the large primary and secondary tubules with their glomeruli, with large irregular spaces lined by a single attenuated layer of endothelial cells. Frequently a few blood corpuscles may be seen in these spaces. On the upper and inner side of the lobe, however, we still find a dense mass of blastemic cells from which tubules and glomeruli are still developing. I am not disposed to say that tubules never branch but it appears rather from the above observations, that they arise independently, but in the course of growth may come into contact and fuse with other tubules. In stage XIX the cells of the lower part of the tubules have increased greatly in size and those of the lower and second curve are enormous compared with their original size. In most of them the large nucleus is clearly visible and some are filled with densely staining granules. The cells of the duct have grown comparatively little. This development seems always to begin at the lower end and to extend gradually upwards. The kidney lobe is large and its wall is composed of extremely flat, thread-like cells.

Glomerulus.

The blood supply of the first ten somites has been discussed under the head of pronephros and we may now consider more in detail the conditions which obtain further back. As mentioned before, in IV (1) in the tenth somite and for a short distance further, we find a vascular tuft within the tubule which we must consider the first appearance of the glomerulus. The first trace of this tuft is seen in a tubule at the end of somite nine before the lacunae of the glomus have disappeared. The two conditions, therefore, overlap. On the dorsal side of the median end of the tubule there is a thick mass of dense staining cells which extends into the lumen of the tubule as a projecting tuft. The cells are less dense at the outer edge and are seen to be very round and loosely held together, though there are no spaces. In some tubules the tuft looks like three or four bunches of grapes in a cluster. In most of the embryos of about this age, however, this tuft is not found regularly on the median

dorsal wall of the last tubules of the tenth somite, but similar cells in smaller groups may be seen projecting into the coelom, or irregularly placed about the end of the tubule. Beyond the tenth somite the glomerulus always arises at this point in primary tubules. In stage XII the wall of the end of the tubule where the glomerulus is found is formed by a single layer of flat, thread-like cells and is sometimes difficult to find. The cellular nature of the external glomera of the late stages of the pronephros is probably due to the fusion of these irregular advance cells of the glomerulus with the lacunae of the glomera.

At first there is only a single glomerulus on either side, but at stage XVI we find three, one above the other, and they undoubtedly continue to increase with the continued development of the tubules. They do not, however, develop so fast as the tubules; for in embryo XII (3) it will be noted that the glomeruli dwindle and cease while the tubules are still large. At this time and later their structure is slightly irregular, as may be seen from Fig. 1, Plate 5.

The earlier branches from the aorta to the lacunae stopped at the tenth somite, and it is not until some time later that the aortic branches to the glomeruli appear. Up to stage XVI they are very small and it sometimes seems almost as if the blood corpuscles push their way through the tissues from the aorta to the glomeruli. From this point on, one always finds many corpuscles in the glomeruli, so that at times the tissue can scarcely be seen at all.

The essential characteristics of glomus and glomerulus respectively may be classified as follows:

Glomus.	Glomerulus.
1. Origin: lacunar evaginations from the aorta.	1. Proliferation of cells from wall of tubule.
2. Extent: 6th—10th somites.	2. 10th somite to near cloaca.
3. Positions outside and around tubules.	3. Within the end of the tubule.
4. Lacunae may anastomose and glomera become more or less united.	4. Glomeruli remain distinct.
5. In late stages becomes external.	5. Never external.

The mesonephros is composed of non-segmental tubules arising from the middle plate from about the 2nd somite to near the cloaca, which in the pronephric region generally fuse with pronephric tubules, and open into the coelom at the median end and the duct at the

other; through the remainder of the body they are closed off from the coelom and have a glomerulus, fed by branches from the aorta, dependent from the dorsal wall of the median bubble-like end; they early become S-shaped, but increase in number, irregularity and size of cells with development.

Metanephros.

The first indications of the coming metanephros are found in embryos of stages XI and XII. The *Platypeltis* embryo XII (4) [Plate 4 Figs. 7—12] shows the earliest stage of the branching of the ureter from the dorsal wall of the duct at its opening into the cloaca. Here the evagination of the dorsal wall at first shows only a less rounded contour, which is hardly noticeable and one would not remark the more pointed outline in the following sections except for what is seen in later stages. The small size of the blastema of denser staining cells just outside the wall of the evagination is very striking. Considered by itself one would almost certainly interpret it as arising from the division of the cells of the wall or to as due the stimulus (mechanical or chemical) of the cells pushing against it. The reduced and irregular blastema of the mesonephric tubules lies on the median side of the developing ureter. In *Platypeltis* embryo XII (2), if we follow a few sections beyond the first point of the opening of the Wolffian duct into the cloaca, we see a sudden outgrowth in the dorsal wall pushing directly up into a small but compact blastema of denser staining, concentrically arranged cells, lying just above the duct. Here, too, a careful study will separate the blastema of the metanephros from that of the mesonephric tubules, which is in contact with it. Following the blastema to the anterior end we find several cells in mitotic stages at a marked distance from the mesonephric rudiment, which is clearly not the centre of growth for the new blastema.

Plate 4 shows the condition in an embryo of stage XI (Figs. 1 to 4) and two sections also from one of stage XIV (Figs. 5 and 6). A most careful study of sagittal series of this and later stages gives similar results. As the ureter pushes forward and the blastema around it becomes larger, the end of the mesonophric blastema is for the space of two or perhaps three sections so closely connected with it that from such older stages it would be impossible to determine a separate origin for the metanephric blastema. From such series and from a more cursory glance at those just described, I was for months in doubt as to the true condition. The lack of sufficient reason for

the growth of the remnant of the mesonephric blastema in the opposite direction to its original development after it has become so very circumscribed, and the fact of the very short connection between the two blastemata (not more than three sections at most) led me to make a more careful examination, and I am now satisfied that the origin of the metanephric basis is not the mesonephric blastema, although it may receive a few cells from the latter.

In examining the development of the metanephros, sagittal sections, Plate 6, were found very valuable. Here one finds the dense blastema lying above the mesonephros in the connective tissue between the lining of the coelom and the vertebrae. It is sharply outlined, and separated from the mesonephros in the early stages by a considerable layer of connective tissue. The ureter pushes further and further forward, but it is always preceded by the blastema which ends in a typical cluster of concentrically arranged cells. The ureter extends over two thirds of the length of this blastema, though it does not appear so long in this drawing.

There are no signs of tubules until the blastema is about one third as long as the metanephros, and then there appear thickenings in the blastema alongside the ureter but distinct from it. These very closely resemble the mesonephric tubules in their early development except of course that the order is from behind forward instead of the reverse. They very soon come into contact with the ureter and open into it. On Plate 5, Figs. 2 and 3, are drawings from an embryo of stage XVI, at the posterior end of which metanephric tubules are developing independently, while further forward they seem to be branching from the ureter. Cross and frontal sections were also examined and confirmed the independent origin of the posterior tubules. With the continued growth of the metanephros, the whole mass extends ventrally and presses against the upper side of the mesonephros. After some of the tubules are clearly formed, however, there still remains the separating layer of connective tissue, and after the mass has become quite large, the two regions are readily distinguished by the difference in the size of the tubules and the character of the cells, although by this time it may be difficult to follow the exact line of separation in cross sections.

Here we see an organ growing backward, contrary to the laws indicated by a study of all the previous development from the time the embryonic layers were formed. It is impossible to avoid conjecture as to what is the cause of such a strange proceeding. Ponder-

ing about this, the following facts seemed to me to throw some light on the subject: 1) Even in stage XIX, while the metanephros is little more than a basis, the mesonephros appears to have reached the height of its development, the nephric lobe is very large, and leaves little space in the body cavity, the tubules consist of large cubical cells, certainly not capable of much further growth, and we see no mitotic figures. 2) In stage III, the neurenteric canal is but fifteen sections (150 μ) behind the opening of the Wolffian duct into the cloaca, therefore, this is the region from which the mesodermal sheet first grew forward, and where, if at all, we should expect to find embryonic cells. 3) The appearance of the tissue is that of embryonic material, with its close-packed, densely-staining elements.

If one may venture to speculate a little, it seems as if the growth of the embryo demanded a better excretory system. The mesonephros had reached its highest possible development and could not grow and meet the new demand, all the embryonic tissue in the anterior end of the body had been appropriated by the various organs and there was no room in the body cavity for another kidney. The point at which the new growth begins seems to be the only one where the increasing need, whatever the stimulus, could be met by the formation of another organ.

The conclusions reached by means of these researches may be summed up as follows:

1. The pronephros of the turtle arises as outgrowths from the posterior somatic region of the somites, having the fourth and tenth as its anterior and posterior limits, respectively, and shows such variation and irregularity as is to be expected in a rudimentary organ. The posterior tubules more or less fused with mesonephric elements, function as excretory organs.

2. The mesonephros of the turtle may extend anteriorly over much of the pronephric region and fuses with it so that the parts can only be distinguished in the earliest stages.

3. a) The metanephros has its origin where the ureter branches from the upper side of the Wolffian duct and in the blastema surrounding it.

b) Apart from this point of union, and perhaps a few cells from the mesonephric blastema the metanephros arises in entire independence of the mesonephros.

c) The tubules of the metanephros arise independently in the

blastema surrounding the ureter and probably also as branches from it.

4. If the foregoing hold true, then pronephros, mesonephros and metanephros are heterodynamous, not homodynamous organs, connected alone by their relations to the Wolffian duct.

5. The glomus of the pronephric region is distinct in origin, character, position and extent from the glomerulus of the metanephros.

Literature.

Among the most important papers on the urinogenital system of Reptiles are those of Max Braun[1]), C. K. Hoffmann[2]) and of R. Wiedersheim[3]). Max Braun used lizards and snakes and C. M. Hoffmann lizards. Max Braun gives a review of all the literature preceding his article, and is in turn, with others, reviewed by Hoffmann. Braun was the first to establish the development of the ureter from the dorsal side of the Wolffian duct. The basis of the metanephros, he finds in disconnected strands of cells. He thinks they originate from the peritoneum, but as they extend beyond the region of the body cavity, Hoffmann questions it. Both Braun and Hoffmann find the metanephric tubules developing as branches from the ureter.

Hoffmann has earlier stages and finds (p. 264) "die erste Anlage bei *Lacerta agilis* in der Bildung einer segmentirten Falte oder einer Reihe segmentaler Ausstülpungen der Somatopleura, welche sich dort bildet, wo der Somit in die Seitenplatte übergeht; dieselbe erstreckt sich unter 6—7 Somiten, die Zahl derselben scheint nicht immer constant zu sein", and on page 265: "Es scheint mir nun wohl nicht zweifelhaft, dass diese . . . die Anlage eines rudimentären Pronephros vorstellt." He finds also that the posterior of these grows backwards and forms the "Anlage" of the Wolffian duct and unites so closely with the ectoderm that it is difficult to tell whether it is a case of true fusion or not. The later stages of the pronephros seem to be quite different in lizards from the conditions I find in turtles. He finds the "Anlage" of the mesonephros just as it is de-

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1) Das Urogenitalsystem der einheimischen Reptilien, in: Arb. zool.-zoot. Inst. Würzburg, 1877—78, V. 4.

2) Zur Entwicklungsgeschichte der Urogenitalorgane bei den Reptilien, in: Z. wiss. Zool., V. 48, 1889.

3) Ueber die Entwicklung des Urogenitalapparats bei Crocodilen und Schildkröten, in: Arch. mikr. Anat., V. 36, 1890.

scribed by Van Wijhe and Rückert for sharks, and says (p. 271): "Among the lizards there are also mesonephric tubules in the region of the pronephros . . . they run into full connection with the pronephros", and he describes just such cases of two tubules side by side, as have been mentioned above. I am interested to see that I have interpreted them in the same manner, although I did not have his conclusions in mind at the time. Under the description of the mesonephros, he says (p. 275): "Schon in sehr jungen Entwicklungsstadien schickt der Theil der Wand eines Malpighi'schen Körperchens, der dem Ansatz des Halses gegenüber liegt, einen soliden zelligen Fortsatz medialwärts ab, der sich dann dorsal- und ventralwärts verlängert, die dorsale Verlängerung bildet die Anlage der Nebenniere", in the description of the metanephros itself (p. 290), however, he makes no such statement, and leaves the origin of the blastema unsettled.

Wiedersheim had crocodiles and turtles for his material, but no very young stages, and so, although he argues from many points that the anterior region must be a pronephros, yet he, naturally, could not distinguish it from the mesonephros. In his conclusions he says (p. 461): "Vorniere und Urniere gehen ohne sichtbare Grenze in einander über und es war, an keinem Präparate auszumachen, wo jene aufhört und diese anfängt. Aus diesem Grunde konnte auch die Trichterzahl jedes Organs für sich nicht genau präcisirt werden." With regard to the origin of the tubules, however, Wiedersheim claims that they are formed by abstriction from the coelom (p. 437 No 2): "und die wohl als Abschnürungen des Cöloms zu deuten sind." He says that the metanephros of the two species of turtle he examined, was exactly the same as in the crocodile. Of the metanephros of the crocodile, he says (p. 446): "Jene Zellen nun hängen mit dem Epithelgewebe des hintersten Urnierenabschnittes durch solide Stränge continuirlich zusammen. Eine Grenze zwischen beiden lässt sich nicht ziehen." . . "Das ganze Bild lässt sich nicht anders deuten als im Sinn einer vom hintersten Urnierenende in dorsaler Richtung vor sich gehenden Sprossenbildung mit secundärem Durchbruch in den Ureter." . . . . "die erste Anlage der drüsigen secernirenden Nierenelemente durch einen Anstoss von der Urniere, nicht aber vom Metanephrosgang, vom Ureter, aus erfolgt. Die Urniere und die bleibende Niere ist also . . . histogenetisch eines und dasselbe." It seems to me as if such a conclusion could be reached only by examining late stages.

The researches of HOFFMANN, WIEDERSHEIM and myself show interesting similarities in regard to the pronephric region; with regard to the basis of the mesonephros and the formation of tubules, my results correspond with HOFFMANN's save that in *Platypeltis* one does not see the early separation from the side plates found by him in *Lacerta*. HOFFMANN and WIEDERSHEIM derive the secondary tubules of the mesonephros by branching from the primary tubules, but my material shows at least one entirely independent series of secondary tubules. BRAUN and myself have obtained results entirely at variance with those of WIEDERSHEIM and HOFFMANN as to the origin of the metanephros finding no direct connection with the mesonephros, but the conditions in the form studied by BRAUN are entirely different from those I find in *Platypeltis*.

In comparison with the work on other orders, it will be seen that my results as to the origin of pro- and mesonephros are entirely in harmony with those of RÜCKERT and VAN WIJHE in their work on the shark, and support the same conclusions, although, as HOFFMANN also noticed, the lumina of the tubules, in our material do not correspond with those of the somites.

There is nothing in my material which would justify the title of "Vornierenkammer" as found by MAAS and SEMON in *Myxine*. Although the lacunae of the pronephros sometimes anastomose — they run irregularly through the body tissue near the tubules and are not circumscribed or confined by a wall of any sort except the wall of the coelom. When they acquire tissue, possibly from the combination with mesonephric elements, they seem to push out further into the body cavity and from more or less continuous external glomera, largest near the funnels.

From the fact that I find no glomerulus in the pronephros (save exceptionally in somite X as explained above) and no tubules opening into the body cavity in the mesonephros, it is clear that I find no "Innen- und Aussentrichter" as described by SEMON, '92 (tab. 3, fig. 7), and discussed by FELIX, in: Anat. Anz., V. 13.

It seems to me that the most important bearing which my work has on that of PRICE is in the fact that it shows how early the marks distinguishing pro- and mesonephros may be lost, though clear in the beginning, and that, therefore, since he says, '97, p. 212: "Even in the youngest embryo the myotomes are entirely separated from the unsegmented portion of the coelom and throughout the greater part

of the system the tubules are already formed"; it is plain that his material was not young enough to determine finally their homology.

With the imagination I can suppose that the external glomera may by entering the later closed off tubules become the glomeruli of the mesonephros, as is held by some. Felix in the discussion over *Myxine* (in: Anat. Anz., V. 13, p. 593) says: "Die Vorniere kann also einen Glomerulus besitzen, der vollständig mit dem der Urniere übereinstimmt", but I can find no such relation in my material. If they were one and the same structure, at the point where the glomeruli first appear, they should be in the same condition as the glomus but such is not the case. The glomerulus appears as described above, as a large tuft of cells developing from the inner dorsal wall of the tubule. These cells are very round while outside of the tubules the glomera do not contain tissue.

Here I am in harmony with Maas, who says, '97, p. 498: "Das Verhältniss, das die Vornierencanälchen zum Glomus haben, diesen letztern Beziehungen der segmentalen Urnierencanälchen zu den einzelnen Glomeruli homolog zu setzen, dürfte wohl unmöglich sein", and again, p. 501: "das 'Glomus' der Vorniere, so wie es entwicklungsgeschichtlich gefunden wird, und dessen Hineinragen ins Cölomdivertikel gerade zum Vergleich mit dem Glomerulus in der Bowman'schen Kapsel Anlass gegeben hat, eine ganz secundäre cänogenetische Bildung ist und mit dem Wesen einer Vorniere gar nichts zu thun hat." Semon holds very strongly to the close relationship, but a study of his figures, '92, figs. 1 and 2, shows such dissimilar structures that it seems to me impossible to homologize them.

In connection with the Cölomtasche described by Price, '97, I may say that in some of my embryos when the basis of the anterior limb has grown and folded down so as to form a small and sharp corner with the kidney lobe, simulating a tubule, I find occasionally that the endothelium has thickened here and looks as if a second one would form or was forming there. This appearance is soon lost, however, and in no case could a true tubule be demonstrated.

Incidental Observations.

In the course of such a study and the examination of so many series of slides, I have necessarily noticed interesting points not related to my subject. It may be worth while to mention one or two of these.

The earliest stages were exceedingly interesting for cell study,

offering some apparently anomalous cases of division especially in the periderm; one case of division of a primitive ovum was observed.

More interesting, however, was it to find a structure apparently exactly like that recently studied by A. Prenant, and which he compares to the hypocord of Ichthyopsida.

In view of the studies of coloration recently made by Th. Eimer and others, I will give briefly the development of the color in *Platypeltis*. The first indication of external color is the appearance of a single row of dots at regular intervals along each side of the spinal column. These become quite dark round spots before others come. Then similar markings appear at irregular intervals between these and the edge of the carapace. But the definite number seems to be established while the remainder of the embryo is perfectly white. At a somewhat later stage the whole of the embryo aside from these dots acquires suddenly a uniform pale gray tint which gradually becomes more opaque, but not dark. The dorsal side is darker than the ventral which at some time after hatching turns white. The original spots remain, but except on the head and around the edges each appears to spread so that before hatching it becomes a small circle of dots which may have one or a cluster in the middle. These seem to develop proportionately with the growth of the turtle and a turtle a foot long showed no change in the character of the color except that the under side of the carapace had become white. I have seen much older turtles, eighteen inches and more long, in which the general body color seemed to have deepened so as to conceal the markings for they appeared a very dark uniform brown or black, but I have not followed the changes here.

Some may care to know the order in which motion is developed. The first motion which I detected was the flexing of the heed ventrally from the point where the neck joins the carapace. Later the mouth may gap and close but aimlessly. After the embryo has acquired color and seems quite a turtle, it draws back the head towards the carapace and opens and closes the mouth with definiteness. The fore feet complete their development first and immediately take the swimming motion if the animal is put in any liquid. The hind feet follow as soon as developed. From these facts it is clear that a turtle does not need to be taught how to draw in the head to bite or swim.

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Description of Plates.

Plates 1—6.

Abbreviations.

a cells for walls of aorta	*l.b* lung buds
a.b aortic branch	*mes* mesonephros
ao aorta	*mes.b* mesonephric basis
b basis	*mes.bl* mesonephric blastema
bl blastema	*mes.t* mesonephric tubules
c.a caudal artery	*met.bl* metanephric blastema
c.d collecting duct	*met.t* metanephric tubules
ch chorda	*my* myotome
cil cilia	*n* nerve
coel coelom	*n.c* neural cord
c.t closed tubule	*oes* oesophagus
c.v cardinal vein	*o.t* open tubule
d duct	*ov* primitive ova
ect ectoderm	*ov.d* blastema of oviduct
ent entoderm	*ph* pharynx
f funnel	*pr.b* pronephric basis
gl glomus	*pr.t* pronephric tubule
gli glomerulus	*som* somite
h heart	*w.d* Wolffian duct.
i intestine	

Plate 1.

Cross sections of *Aranochelys* embryo of stage II, showing the pronephric welt (*pr.b*) extending from the 6th to 10th somites.

Fig. 1. Somite 6, section 1.
Fig. 2. „ 6, „ 5.
Fig. 3. „ 6, „ 8.
Fig. 4. „ 6, „ 9.
Fig. 5. „ 6, „ 10 (between somites 6 and 7). Pronephric welt continuous and position of mesonephric basis (*mes.b*) in the middle plate is clearly seen on the right.

Figs. 3—5 show cells (*a*) slipping from the sclerotome to form the walls of the aortae.

Fig. 6. Somite 7, section 6.
Fig. 7. „ 7, „ 9.
Fig. 8. „ 7, „ 10 (between somites 7 and 8).
Fig. 9. „ 8, „ 6. Beginning of lumen in the tubule on the left.
Fig. 10. Somite 8, section 11 (between somites 8 and 9).
Fig. 11. „ 9, „ 4 (5—8 are similar).
Fig. 12. „ 9, „ 11 (between 9 and 10).
Fig. 13. „ 10, „ 4.
Fig. 14. „ 10, „ 6. End of segmentation.

Figs. 15—17. Cross sections from *Platypeltis* embryo B II (1) showing pro- and mesonephric bases (*pr.b*, *mes.b*).

Fig. 18. Same as Fig. 5.

Figs. 19—26. Cross sections from *Platypeltis* embryo II (1). This is more advanced than the first series and the distinction between pro- and mesonephric tubules is very clear. In some cases they can be seen opening side by side into the body-cavity, in others one funnel serves for both rudimentary tubules.

Fig. 27. End of right Wolffian duct (*d*) of an embryo of stage II.

Figs. 28—29. Ends of left and right Wolffian ducts (*d*) of an embryo of stage II.

Plate 2.

Figs. 30—39. Cross sections from *Platypeltis* embryo B II (1), showing the pronephric welt developed from separate outgrowths (*pr.b.1*, *pr.b.2*, *pr.b.3*, *pr.b.4*), the formation of aortic walls *ao* and very numerous mitotic figures.

Fig. 30. Som. 5, sect. 9.
Fig. 31. „ 6, „ 1.
Fig. 32. „ 6, „ 9.
Fig. 33. „ 6, „ 10.
Fig. 34. „ 7, „ 5.
Fig. 35. Som. 7, sect. 6.
Fig. 36. „ 7, „ 7.
Fig. 37. „ 7, „ 11.
Fig. 38. „ 8, „ 3.
Fig. 39. „ 9, „ 7.

Figs. 40—47. Cross sections from *Platypeltis* embryo III (5), somite 7, sections 3—10, showing pronephric (*pr.t*) and mesonephric tubule (*mes.t*) developing side by side and having separate openings into the coelom. The lacunae of the glomus are seen in each section and in 42—44 an aortic branch by which they are fed.

Plate 3.

Figs. 48—51. Cross sections of *Platypeltis* embryo V (2).

Fig. 48. Combined from sections 1 (left) and 2 (right) of somite 8, shows tubules opening into the coelom (*o.t*) on either side and lacunae of the glomera. The cells of the tubules are much larger than in earlier series.

Fig. 49. Combined from section 18, somite 8 (left), and section 1, somite 9 (right). The increased irregularity of tubules is marked. On the right is an aortic branch (*a.b*).

Fig. 50. Section 18 of somite 9. Tubules on each side almost closed by the distended lacunae of the glomera.

Fig. 51. Section 9 (left) and section 8 (right) of somite 10. On the right is the last tubule opening into the coelom (*o. t*) and on the left is the first tubule completely shut off from the coelom (*c. t*). This contains the cell tuft which forms the glomerulus (*gli*).

Figs. 52—56. From cross sections of *Platypeltis* embryo XII (3).

Fig. 52. Section 4 of somite 6, shows on the left the most anterior element remaining of the pronephros (*c. d*), which is non cut off from the coelom and imbedded in the sclerotome near the aorta.

Fig. 53. Section 23 of somite 6. Anterior end of the coelom with glomera and on the left a pronephric tubule.

Fig. 54. Section 1 of somite 7 shows a further development of the cells of the tubule in which densely staining granules are often found. The glomera project freely into the body cavity. They have now acquired more or les cellular tissue but are still little more than a meshwork in which many blood corpuscles are caught. This is not shown by the even yellow tinting.

Fig. 55. Section 8 of somite 10. Last freely open tubules. The cilia (*cil*) are conspicuous.

Fig. 56. Section 16 of somite 10. On the left an incompletely closed tubule with glomus. On the right is the first closed tubule with distended end from which the glomerulus has been lost in handling.

Plate 4.

Figs. 57—60. Cross sections of *Platypeltis* embryo XI (1).

Fig. 57. Anterior end of metanephric blastema (*met. bl*), Wolffian duct (*w. d*) and mesonephric blastema (*mes. bl*).

Fig. 58. Several sections posterior to Fig. 57. The ureter is seen at the lower outside edge of the metanephric blastema.

Fig. 59. Two sections behind Fig. 58. Near the point where the ureter branches from the duct.

Fig. 60. Seven sections behind Fig. 59. Branching of ureter from the dorsal side of the Wolffian duct at the point where the duct opens into the cloaca.

Figs. 61 and 62. From cross sections of *Platypeltis* XIV (1).

Fig. 61. Anterior end of metanephric blastema (*met. bl*), Wolffian duct (*w. d*), mesonephric blastema (*mes. bl*) and rudiments of two mesonephric tubules.

Fig. 62. Ureter (*ur*) and metanephric blastema (*met. bl*), Wolffian duct (*w. d*) and mesonephric blastema (*mes. bl*).

Figs. 63—68. Cross sections of *Platypeltis* embryo XII (4). Earliest stage of the branching of the ureter from the Wolffian duct.

Fig. 63. Mesonephric blastema (*mes. bl*) and Wolffian duct (*w. d*).
Figs. 64—68. Consecutive sections. Figs. 65—67 accidentally of slightly lower magnification than the others.

Plate 5.

Figs. 69—71. From cross sections of *Platypeltis* XVI (2).
Fig. 69. Ureter (*ur*) and metanephric blastema (*met. bl*). Mesonephros consisting of several coiled tubules with three glomeruli on the right and two on the left and with three openings into the duct on the left. Blastemic tissue is still seen on the median dorsal side of the kidney lobe.
Fig. 70. Shows apparent branching of the ureter.
Fig. 71. Forty-one sections before the branching of the ureter from the duct.

Plate 6.

Fig. 72—75. Combined from two sagittal sections of *Platypeltis* embryo XVI (1). The drawing may be made complete by joining the lower end of one figure to the upper end of the following.
Fig. 72. Anterior end of mesonephric region and remnant of glomus of pronephros with pronephric tubules at the anterior end.
Fig. 73. More anterior part of the mesonephros with glomeruli very distinct.
Fig. 74—75. The posterior end of the mesonephros with part of the Wolffian duct and the blastema of the metanephros with a part of the ureter.

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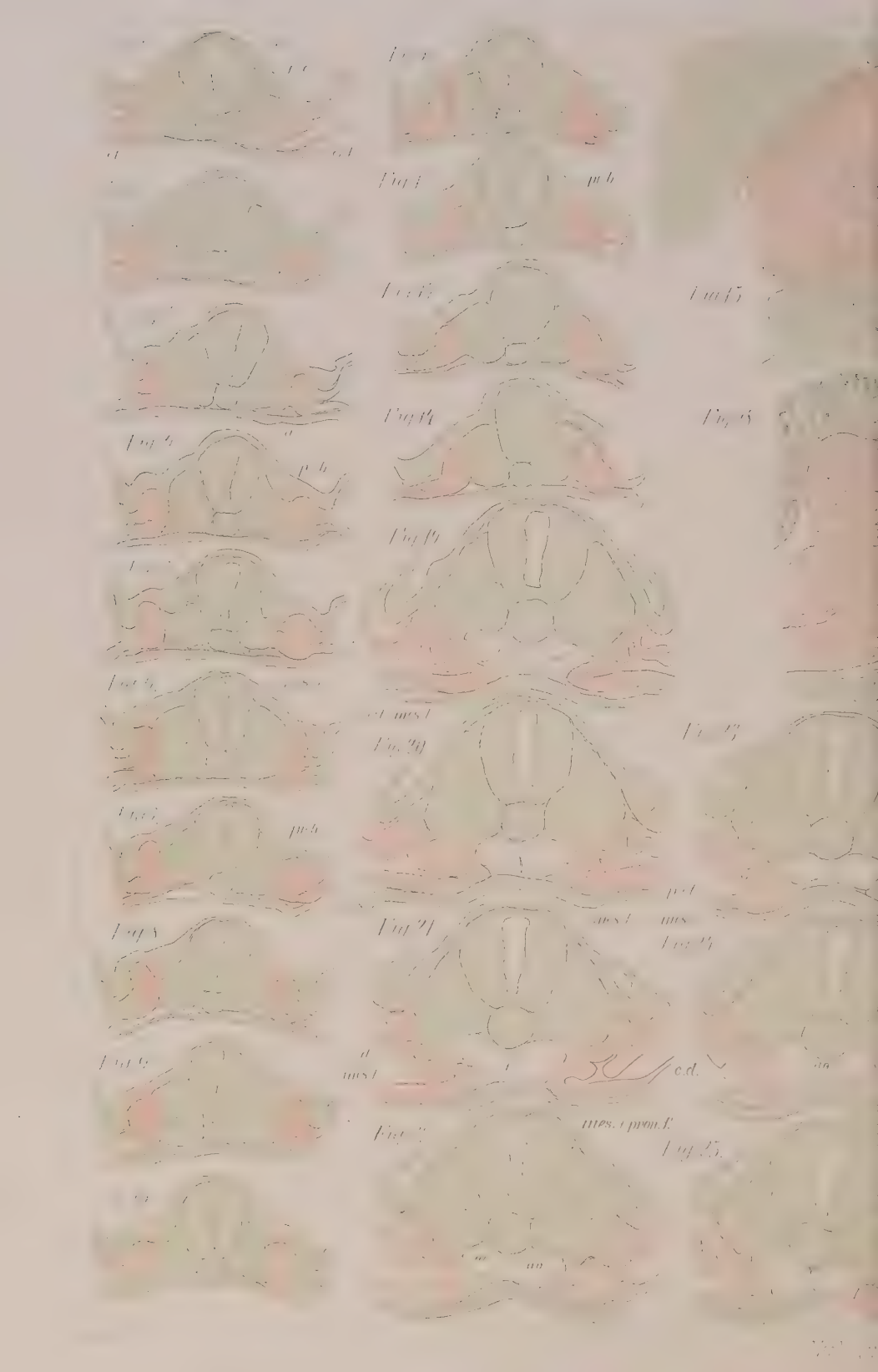

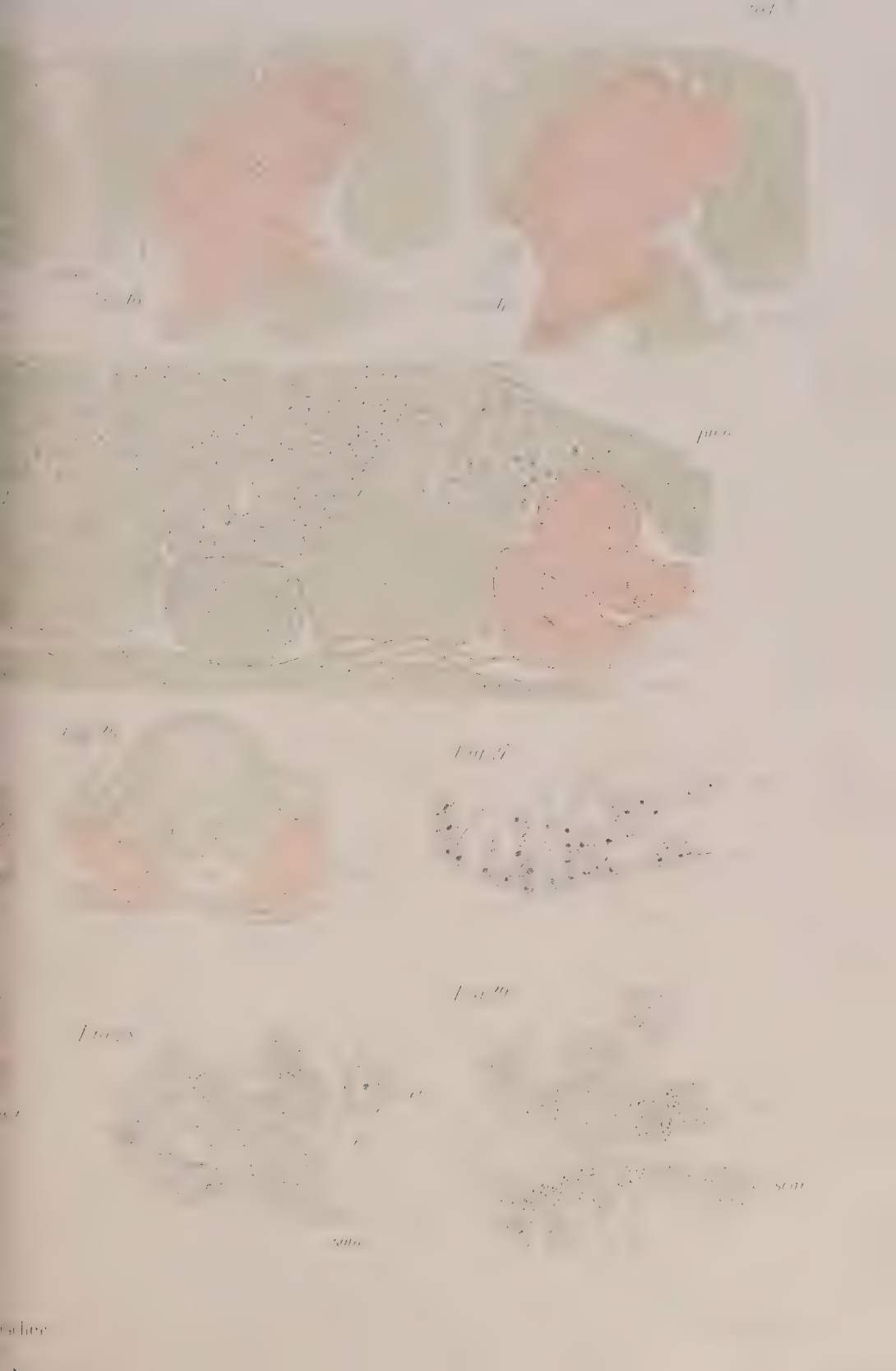

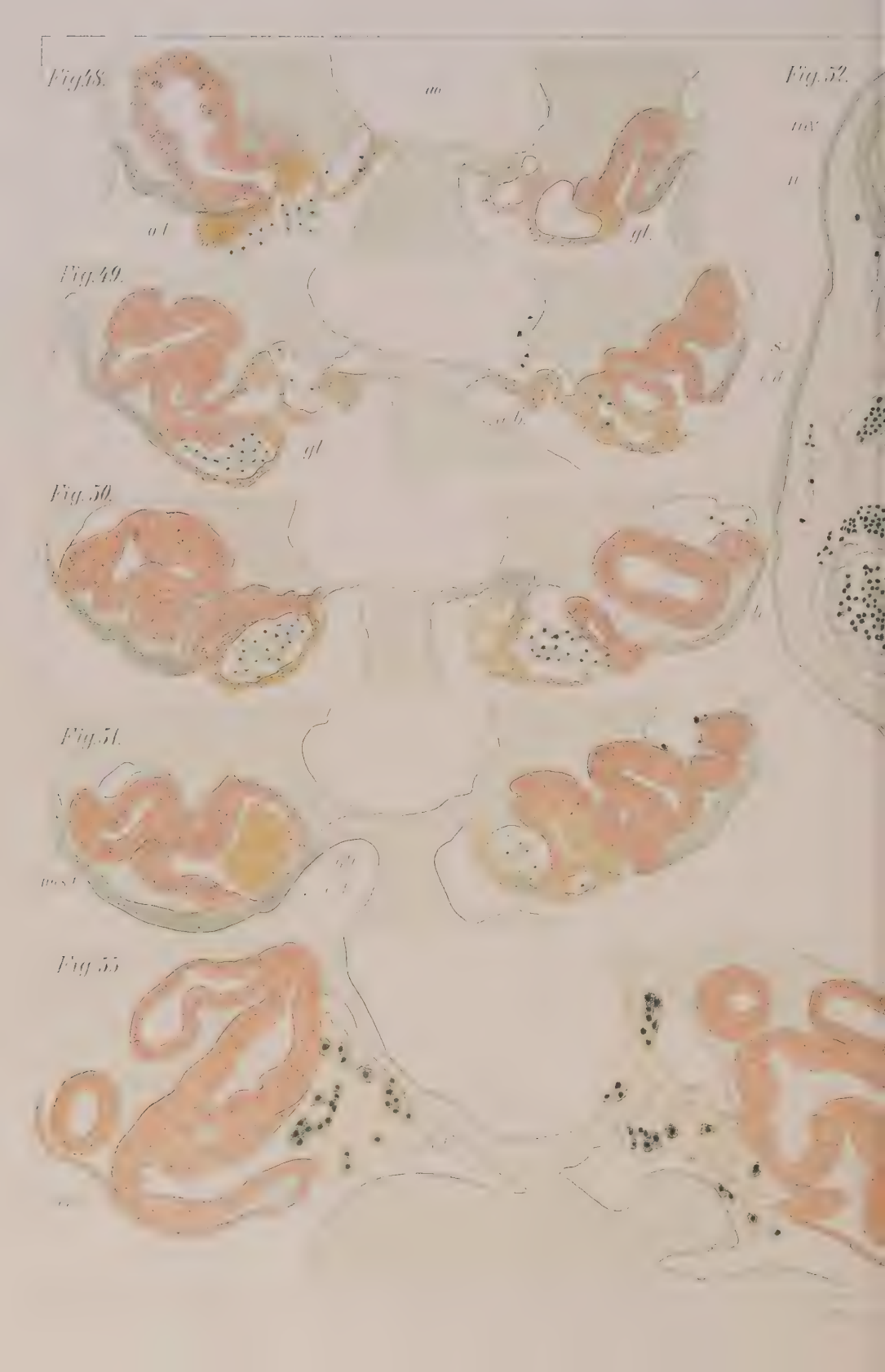
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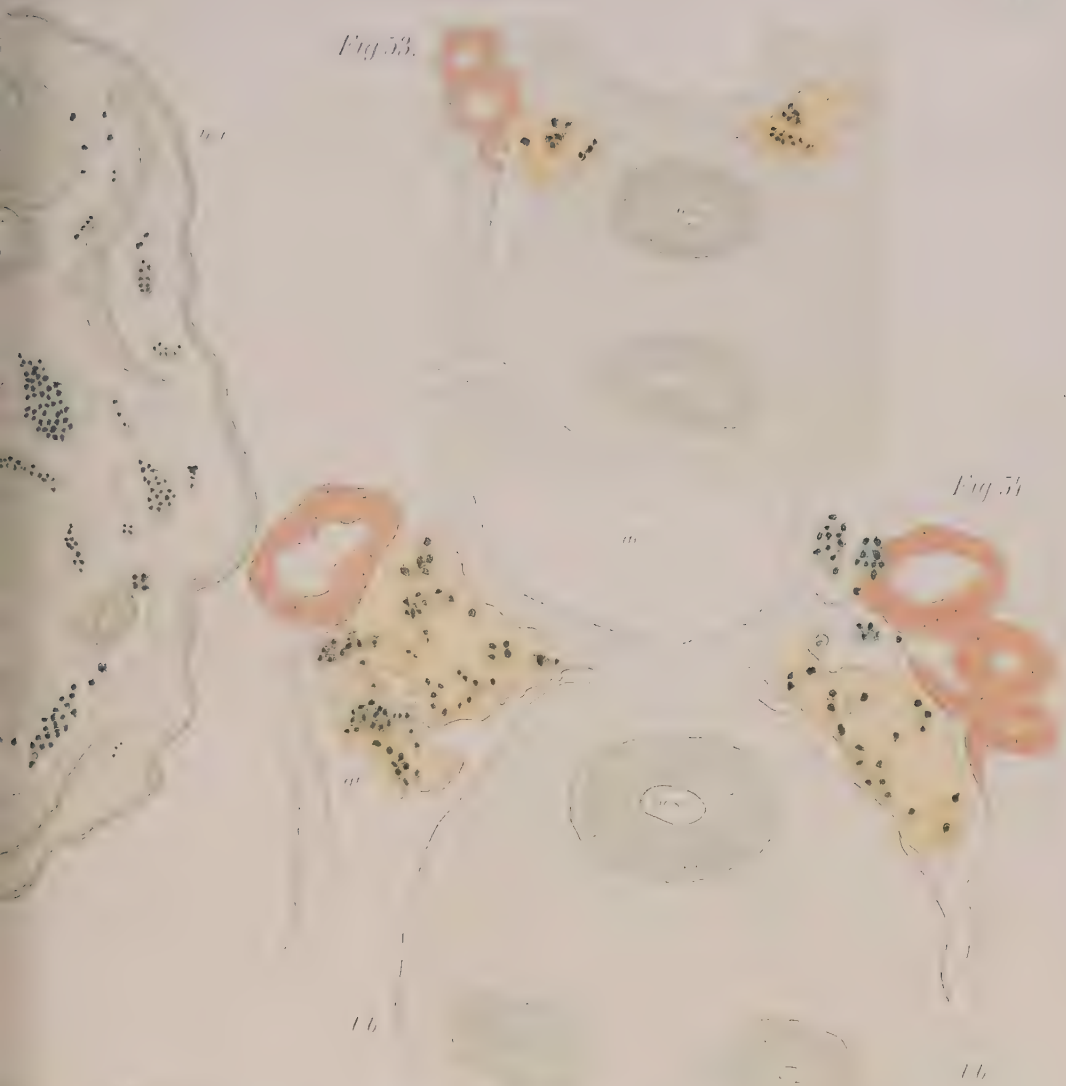

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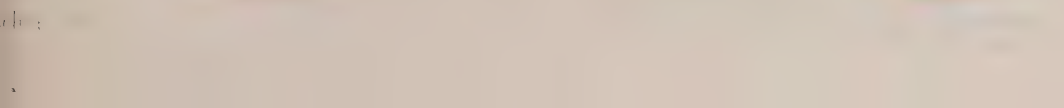

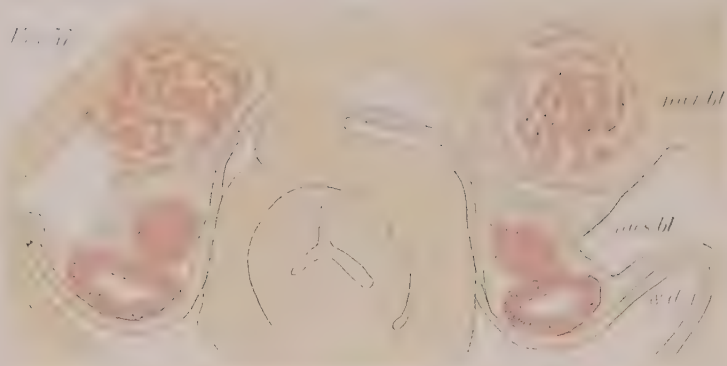

Fig. 61.

Fig. 58

Fig. 62.

Fig. 59.

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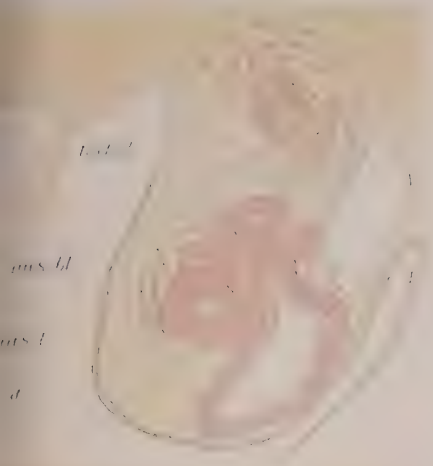
Fig. 64.



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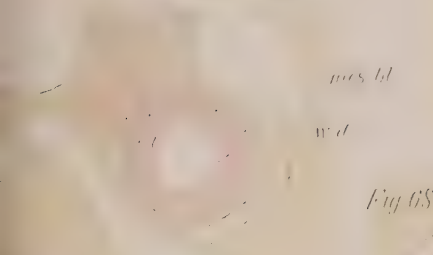

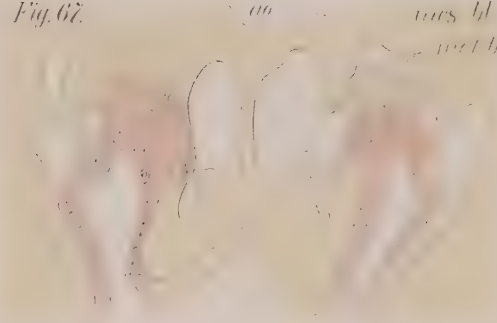

Fig. 68.

Fig. 69.

Fig. 70.

Fig. 11.

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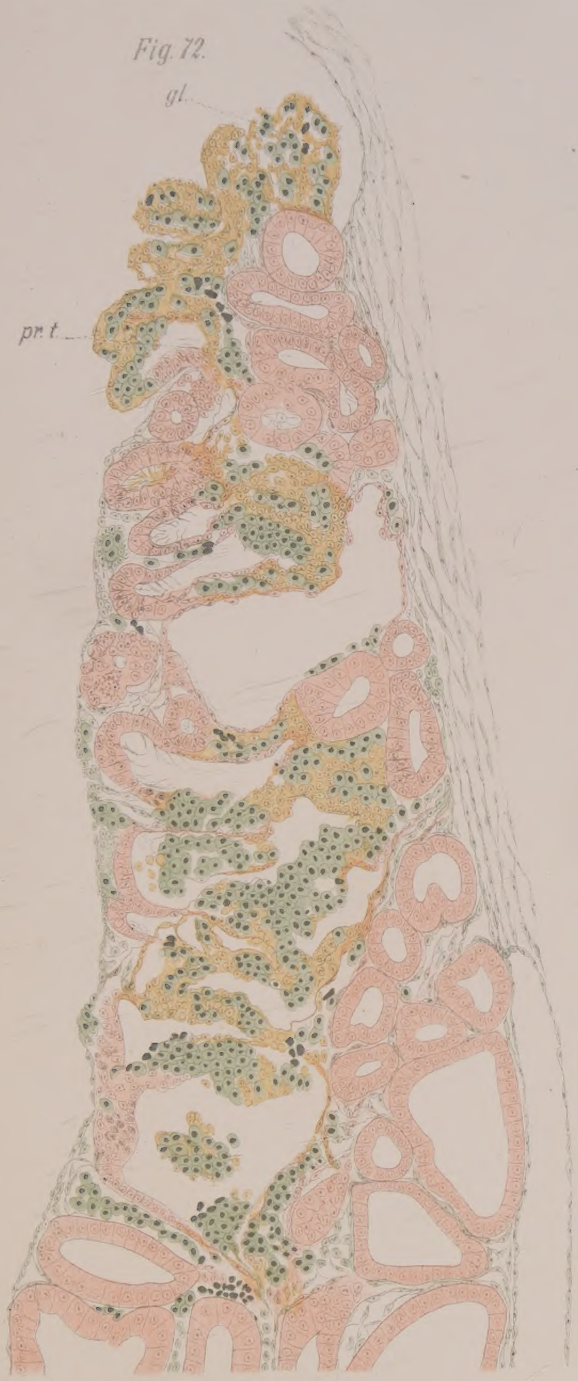
Fig. 72.



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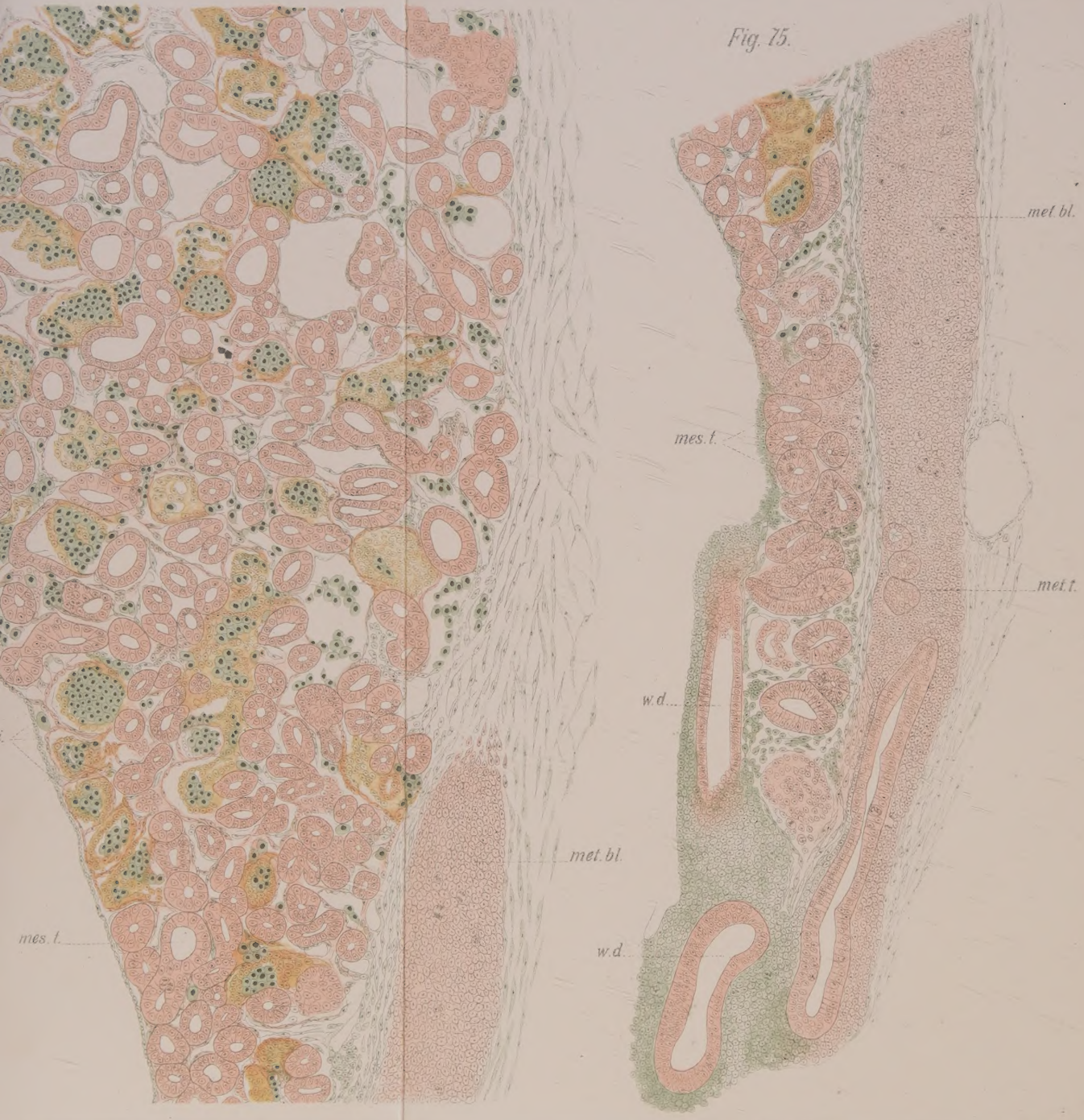

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